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Natural variation in merchantable stem biomass and volume among clones of Populus tremuloides Michx

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Stand density and biomass and volume of merchantable stems were determined and compared for six clones on each of two different sites in Alberta. One site (Blue Ridge) was typically boreal and the other (Nordegg) subalpine. Biomass and volume production at 5 years were significantly different among clones on a shared site and were also significantly different when individual trees were compared between sites. Stocking levels were significantly higher on the Nordegg site at 85 years but not high enough to prevent the Blue Ridge site from producing more biomass (six and a half times as much) and volume (four times as much) on an areal basis. Broad sense heritability estimates suggest that approximately one-third of the variation in biomass and volume of trees growing on each site was genetically based.

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Les auteurs ont déterminé et comparé la densité des peuplements et la biomasse et le volume des tiges marchandes de six clones de peuplier sur chacun de deux sites en Alberta. L'un de ces sites (Blue Ridge) était typiquement boréal, l'autre (Nordegg) subalpin. La production de biomasse et le volume à 5 ans étaient significativement différents entre les clones sur un même site et significativement différents aussi quand des arbres individuels furent comparés entre les sites. Le matériel sur pied était significativement plus élevé sur le site Nordegg à 85 ans mais pas suffisamment pour empêcher le site Blue Ridge de produire plus de biomasse (six fois et demie plus) et de volume (quatre fois plus) sur une base de surface. Les estimations d'héritabilité au sens large suggèrent qu'environ un tiers de la variation en biomasse et en volume des arbres croissant sur chacun des sites est attribuable aux facteurs d'héridité.

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Introduction

Trembling aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America (Harlow and Harrar 1969). Aspen is already an important timber resource in the Lake States but in many areas it has been regarded as a weed species. However, in many of these areas it is presently being considered as a potentially important future timber resource (Johnston and Bartos 1977).

Aspen grows under a wide range of site conditions and shows considerable variation in growth on different sites (Einspahr and Benson 1967; Maini 1968). On poor sites aspen may never attain merchantable size (Maini 1968), but on medium and better quality sites it has been observed to grow more rapidly than associated species (Jones and Markstron 1973).

Throughout its range, aspen stands generally comprise a mosaic of clones (Barnes 1966, 1969; Basham 1958; Copony and Barnes 1974; Fralish 1972; Jones and Markstron 1973; Kemperman and Barnes 1976; Steneker and Wall 1970; Steneker 1972; Wall 1971; Zahner and Crawford 1965). The single stem is the unit of development of most species of North American trees, but the typical unit of growth and development in aspen is the clone. Each clone is a group of genetically identical individuals (ramets) arising vegetatively (through suckering) from a single parent (ortet). Each ramet within a clone has similar phenotypic, growth, and quality characteristics (Barnes 1969; Blake 1964; Einspahr and Benson 1967; Jones and Trujillio 1975*a*, 1975*b*; Steneker 1972; Steneker and Wall 1970; Zahner and Crawford 1965). Zahner and Crawford (1965) and Barnes (1969) documented large differences in growth rates of different aspen clones on a shared site. Graham *et al.* (1963) commented that differences in clonal growth rates could provide foresters with opportunities for genetic selection. If the differences are significant it may be wise to manage aspen on a clonal basis, promoting superior clones, rather than on a stand basis.

Aspen occurs in a broad range of environments. Presumably, this growth is made possible by a wide range of genotypes. It is possible, however, that morphological variation may simply be a response of the species to microenvironmental conditions at the site.

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For management of the species it is important to be able to determine the relative effects of site and genotype on growth.

The objectives of this study were to examine various traits of aspen which relate to potentially merchantable biomass and volume production and to analyze them in terms of probable management strategies. To accomplish these objectives, the stocking and size of aspen clones were examined. Inter- and intra-clonal variation in biomass and volume production were studied on two different sites on an areal and individual tree basis. Finally, the relative effects of site and genetic control over production were examined.

Description of study areas

The choice of study sites was based on three criteria. The first was that each study area should have relatively uniform climate, soils, slope, aspect, and drainage throughout. The second criterion was that the stands in both study areas would be approximately the same age. The third criterion was that major environmental conditions at the two study areas would be different.

Based on these criteria, clones were studied in two forest regions: boreal and subalpine (Rowe 1972). The boreal site was located just north of Blue Ridge, Alta. (latitude 54°12′ N, longitude 115°26′ W); and the subalpine site was west of Nordegg, Alta. (latitude 52°25′ N, longitude 116°34′ W).

According to Heinselman and Zasada (1955), Steneker (1976), and Stoeckeler (1960), soil texture and drainage are two of the most important factors influencing site quality for trembling aspen. Steneker (1976) presented a site-quality matrix of soil texture, moisture, and drainage conditions for the species (Fig. 1). This matrix may be used to compare general site qualities of the study areas. According to this classification, Blue Ridge would be considered a good aspen site and Nordegg a poor one.

The Nordegg site is on a fairly steep slope (30–50%) with a southerly aspect. The Blue Ridge site is relatively level. The Nordegg site is located at approximately 1460 m in elevation and Blue Ridge is at 730 m.

Methods and materials

Six clones were sampled at each of the study areas. The key trait used to delineate clonal boundaries was time of leaf flush. Other characteristics used to help identify clones were bark texture and color, stem form, branching habit, and incidence of galls and cankers.

All trees of the same clone were flagged and numbered. A grid was then established through the clone using rows of string placed 3–5 m apart. Field maps showing the location of the stems in each clone were then drawn. Trees within 4–5 m of the clone boundary were also mapped as an indication of intensity of competition. A line was then drawn on the map bisecting the distance between the outermost trees of the clone and their nearest outside neighbour. This line was used to define the clonal boundary.

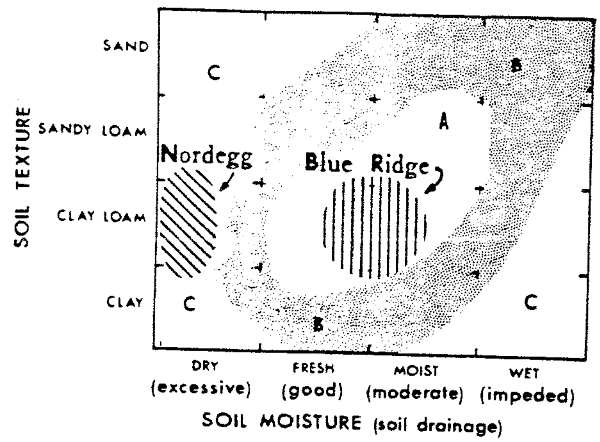

FIG. 1. Matrix of soil texture, moisture, and drainage conditions indicating good (A), intermediate (B), and poor (C) aspen sites (adapted from Steneker (1976)).

Five sample trees were randomly chosen to represent each clone. Sample trees at Nordegg ranged from 77 to 108 years of age while trees at Blue Ridge ranged from 55 to 82 years. Each of the selected trees was destructively sampled for determination of ovendry biomass of the merchantable bole. The merchantable bole was considered to be the segment of the tree from a 0.2-m-high stump to where the stem tapered to 7 cm in diameter or where branching determined the limits of merchantability.

The general procedures outlined in the International Union of Forest Research Organizations (IUFRO) (1971) and Bartos and Johnston (1978) for determining bole biomass were used. Starting at the base, age at stump height was determined from ring counts. The bole was then sectioned into 1-m lengths, whose green weights were measured in the field. The green weight of a 2- to 5-cm-thick disc at the bottom of each section also was measured. The discs were returned to the laboratory, air dried for 2 weeks, and oven-dried for 1 week at 70°C. Tests showed that a constant dry weight was achieved using this procedure. Before ovendry weights were measured, advanced decay was removed from each disc. Advanced decay was considered to be material which could be dislodged from the disc by tapping lightly with the end of a screwdriver. Stain and incipient decay were not measured nor were they subtracted from sound biomass. The following calculations were then carried out to determine the sound biomass of the bole for each tree.

$$[1] \quad \text{Sound bole biomass} = \Sigma \left(\frac{\text{section green weight}}{\text{disc green weight}} \times \text{ovendry weight of sound portion of disc} \right)$$

Volume was determined from DBH and height measurements, using a volume-prediction equation developed by Honer (1967).

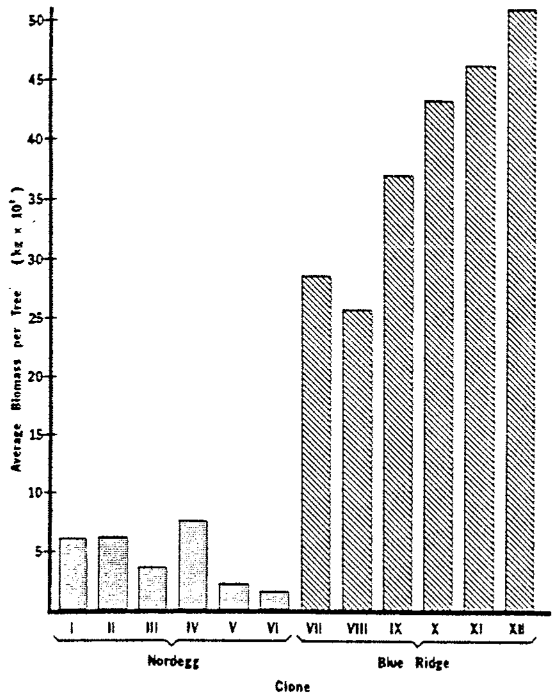

FIG. 2. A comparison of average biomass per tree for clones at Nordegg and Blue Ridge using a base age of 85 years.

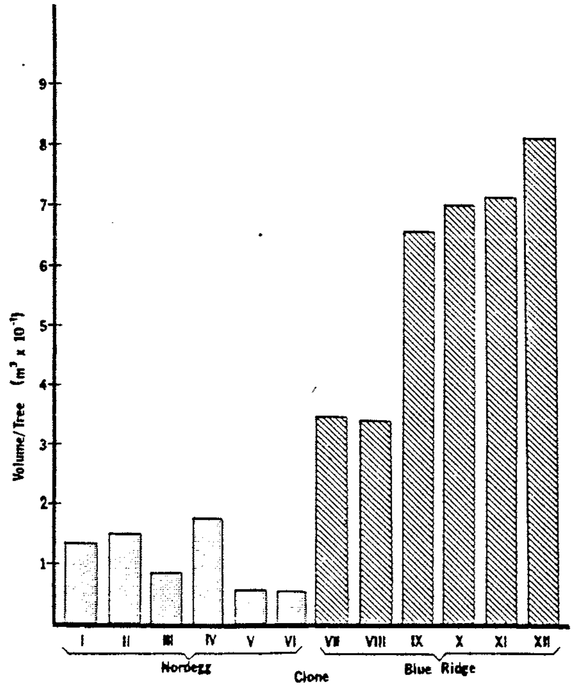

FIG. 3. A comparison of average volume per tree for clones at Nordegg and Blue Ridge using a base age of 85 years.

Statistical methods

Analysis of covariance was used to determine if significant differences occurred in biomass and volume per tree and biomass and volume per hectare among clones on a shared site and between clones on different sites. The *F*-test was applied using 95% confidence limits. Age was used as a cofactor to reduce residual error by adjusting biomass and volume values so that the mass of all trees was based on a common age. The relative importance of environmental and genetic variation on biomass and volume of the trees was analyzed using a broad sense heritability estimate (Zsuffa 1975). This is an estimate of the degree of genetic control of a given trait and is expressed by the ratio between genetic variance and total phenotypic variance as shown in Eq. 2.

$$[2] \quad \text{Broad sense heritability } (h^2) = \frac{\sigma^2 C}{\sigma^2 C + \sigma^2 E}$$

$$\sigma^2 E = \text{error mean square}$$

$$\sigma^2 C = \frac{\text{clone mean square} - \text{error mean square}}{\text{no. of ramets per clone}}$$

All results except the stand-density data are based on adjusted means resulting from the analysis of covariance.

Results and discussion

Size of clones

In Nordegg the size of clones ranged from 0.01 to 0.10 ha with a mean of 0.03 ha. At Blue Ridge the range was from 0.01 to 0.07 ha with an average of 0.04 ha. Since the two study areas are quite different in environmental conditions and show the same average and range in clone size, it appears that site conditions and clone size are unrelated. Steneker (1973) and Kemperman and Barnes (1976) also were unable to find any correlation between clone size and site conditions. Both speculated that clone size was related more to stand history than site. Patterns of initial seeding, disturbance history, competition, and inherent suckering abilities of the individual clones may be some of the factors contributing to present clone size.

Biomass per tree

The objectives of the study dealt with examining differences in biomass and volume per tree among clones on a shared site and among trees on different sites. There were significant differences ($P \leq 0.05$) in biomass per tree among equal-aged clones on a shared site. There were significant differences ($P \leq 0.001$) in biomass per tree between equal-aged aspen stands grown under different site conditions.

Figure 2 illustrates average biomass per tree for each clone on the two sites using a base age of 85 years. The figure does not show intraclonal variability. However, variability among clones and the relative differences in biomass per tree between each of the sites can be seen. The average biomass per tree for Nordegg was 46.3 kg (range of 16.8−76.2 kg/tree). For Blue Ridge, the average biomass was 384.1 kg/tree (range of 256.9−509.6 kg/tree). Average biomass at Blue Ridge was approximately eight times greater than that at the Nordegg site. The Blue Ridge site exhibits considerably more interclonal variation than Nordegg. However, if the relative variation among clones is examined for each site, Nordegg has almost twice the variability of Blue Ridge.

Volume per tree

Calculated volumes were significantly different among clones on a shared site ($P \leq 0.05$) and among clones on different sites. Figure 3 shows mean volume per tree (cubic metres) for each of the clones studied. Average volume per tree at Nordegg was 0.11 m^3 (range, 0.03−0.18 m^3/tree) and at Blue Ridge mean volume per tree was 0.59 m^3 (range, 0.26−0.81 m^3/tree). Average volume per tree was slightly more than five times greater at Blue Ridge. Relative variation among clones is similar to the case for biomass, with the Nordegg site exhibiting the largest amount of variation. The closeness of the relationships between volume per tree and biomass is a reflection of the relatively small quantities of advanced rot in the trees which were studied.

Stocking

A comparison of clonal stocking levels within and between the two sites shows considerable variation occurs (Fig. 4). At Nordegg, stocking ranged from 773 to 2714 stems/ha with an average of 1944 stems/ha. In the Blue Ridge area the range was from 955 to 1766 stems/ha, averaging 1423 stems/ha. The harsher, Nordegg site has an average stocking level almost 50% greater than that at Blue Ridge. In addition, the range of stocking at Nordegg is almost twice that at Blue Ridge. There could be several explanations for this. Because of a combination of climate, edaphic and other site factors, Nordegg has a drier and shorter growing season than Blue Ridge. The Nordegg stand, although close to the same age as the trees at Blue Ridge, appears to have stagnated at an earlier developmental stage. The Nordegg stand may not have undergone the same amount of natural thinning as stands on better sites, since the process of natural stand development appears to take longer on colder and drier sites. There are also a number of opposing factors which could effectively reduce stocking levels in this area. Some clones may not be as well adapted as others to reproduce and fully utilize all available growing space in a harsh environment. Rock outcrops and other natural barriers could also cause openings in the stand. Microhabitat differences occur throughout any area and may also have

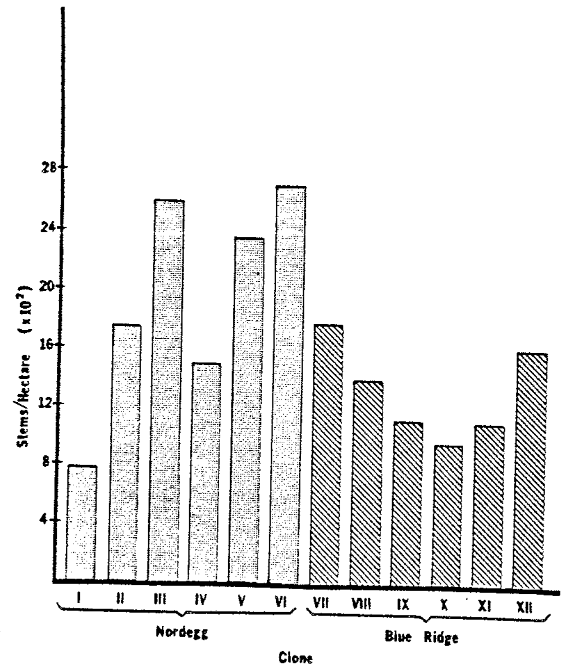

FIG. 4. A comparison of clonal stocking levels within and between the Nordegg and Blue Ridge study sites.

an important influence on whether a tree can occupy the site.

Generally, the clones with the smallest stems also have the greatest stocking levels (Figs. 2 and 4). For example, clones III, V, and VI have the lowest average biomass per tree (Fig. 2). These clones also have the three highest stocking levels (Fig. 4). Barring any severely limiting factors, aspen, or any other plant, generally tends to fully occupy available growing space. Since smaller trees take up less space, more stems would be needed to make full use of the site. The relationship between tree size and stocking substantiates this. There are, however, individual cases which do not follow this trend. Clone XII, from Blue Ridge, has the largest average tree size and also one of the highest stocking levels for the site. Jones and Trujillio (1975*a*) also noted this phenomenon. Perhaps these clones are better suited to the conditions in which they grow. These clones are able to tolerate greater crowding without severely affecting the growth rate of the individual trees. Variations in microhabitat may also influence this variation. Whatever the reason, the trend shown by clone XII suggests seemingly superior productive capability and perhaps, characteristics desirable in a tree selection program.

Biomass and volume per hectare

Baskerville (1965) stated that as stocking increased, overall levels of production increased until full oc-

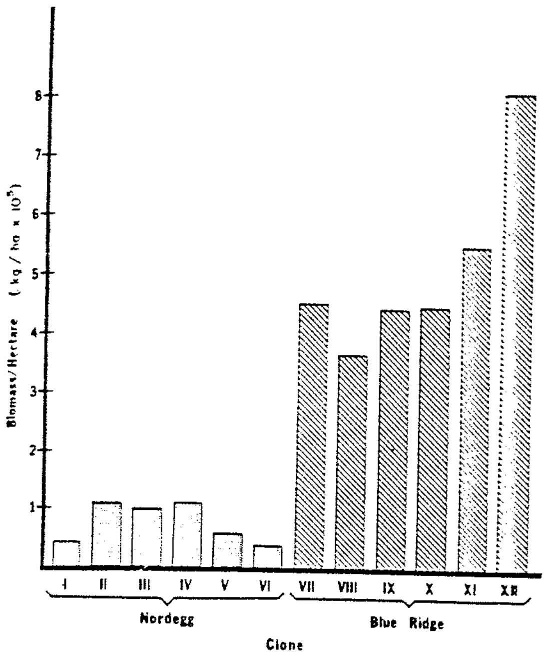

FIG. 5. A comparison of biomass per hectare for clones at Nordegg and Blue Ridge using a base age of 85 years.

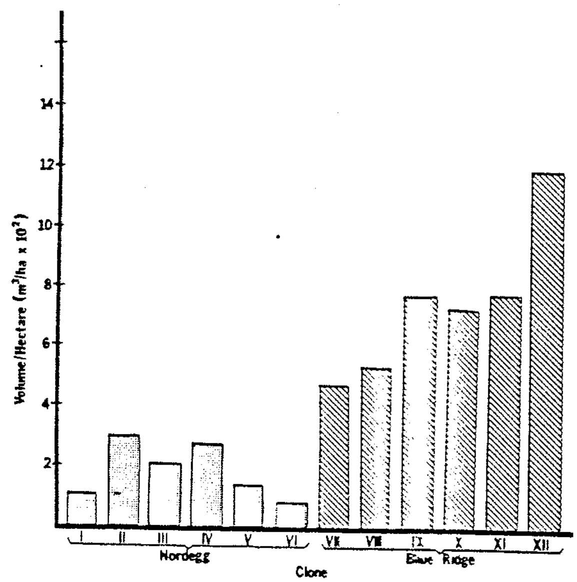

FIG. 6. A comparison of volume per hectare for clones at Nordegg and Blue Ridge using a base age of 85 years.

cupancy of the site was achieved. This would indicate that if the stocking levels of each clone are combined with biomass per tree (biomass per hectare), or volume per tree (volume per hectare), differences in productivity among clones should decrease.

There is a significant difference ($P \leq 0.001$) in biomass per hectare between clones on the Nordegg and Blue Ridge sites (Fig. 5). Biomass per hectare at Nordegg ranged from 39 000 to 140 000 kg/ha with an average of 77 619 kg/ha. At Blue Ridge the range was from 366 000 to 810 000 kg/ha, averaging 510 807 kg/ha.

The average biomass per hectare at Blue Ridge is approximately six and a half times greater than at Nordegg, while the average biomass per tree at Blue Ridge was about eight times greater than at Nordegg. Despite this trend, differences in biomass per hectare between the two sites are still significant. The Blue Ridge site also exhibits a greater absolute range in values among clones than Nordegg.

There is also a significant difference in volume per hectare between the two sites ($P \leq 0.001$). The range in volume per hectare at Nordegg was from 80.3 m³/ha in clone VI to 304.2 m³/ha for clone II (Fig. 6). Figure 6 also shows that volume per hectare at Blue Ridge ranged from 480.4 m³/ha in clone VII to 1190 m³/ha in clone XII. Mean volume per hectare at Blue Ridge was 748.7 m³/ha and was 184.1 m³/ha at Nordegg. Volume production, on an areal basis was, then, approximately four times as great at Blue Ridge. Differences in volume per tree were about fivefold between the two sites meaning reduced stocking levels at Blue Ridge also reduce the potential difference in cellulose produced on the two sites.

The trends noted here are consistent with observations of others. Zahner and Crawford (1965) noted considerable variation in height among clones on the same site. Perala (1977) claimed that variation in yield among clones on a shared site could differ as much as 200%. In this study the yield in biomass per hectare among clones varied from 200 to 300% (Fig. 5). Greene (1971) noted that interclonal variation was greater than intraclonal variation. This implies that on any given site much of the observed variation in productivity among trees is the result of genotype, as opposed to varying site conditions. This is in marked contrast to the study of van Buijtenen *et al.* (1959) who reported that differences in productivity due to genotype were slight when compared with the overall influence of site on biomass production.

Greene (1971) commented that one would expect to find clones exhibiting the greatest variability in productivity on sites where environmental stresses are minimal. Variation in productivity at the Blue Ridge site supports this statement. Poorly adapted genotypes could have been outcompeted and eliminated. On better sites any clone, once established, may persist for a long time.

Heritability

The last objective was to determine the extent of genetic versus environmental control over biomass and volume production. Copony and Barnes (1974) noted that phenotypic differences among trees on the same site are good indicators of genetic differences. In the case of a clonal species such as aspen it can generally be said that differences among trees in the same clone are due to environmental factors whereas differences among clones are due to a combination of site conditions and heredity (van Buijtenen *et al.* 1959). The statistical technique used here to gauge the influence of genotype and environment is broad sense heritability (Zsuffa 1975). Heritability remains constant over time within any given sample population (Mohn and Randall 1971). Therefore, the 10-year difference between ages of trees on the two sites should not influence the results. The clones used in this study were not selected strictly randomly. The choice of clones, then, may influence the heritability and gain estimates.

The broad sense heritability estimate for biomass per tree for Nordegg was 31%. For Blue Ridge it was 35%. The heritability estimate for volume was 40% for Nordegg and 35% for Blue Ridge. This means that about one-third of the total phenotypic variance exhibited was due to genetic control. The differences in estimated heritability for volume and biomass at Nordegg may be a reflection of greater amounts of advanced decay in trees at Nordegg relative to tree size. Removal of advanced decay, of course, reduces biomass estimates but does not affect volume estimates.

The moderate heritability estimates reflect relatively high variation within clones. Kittredge (1938) noted that even in what seems to be a uniform environment, differences in habitat occur, sometimes within a distance of a few feet. These microdifferences in habitat probably play a major role in influencing biomass production. Van Buijtenen *et al.* (1959) also claimed that slight age differences and positioning of suckers on the initial parent root may have some effect on biomass production.

In each of the two sites investigated, there was a large amount of clonal variability in biomass production. The variability may make it possible for clonal programs to produce a gain in productivity in future generations. Our sample size was relatively small, but if we assume that the sample mean is close to the population mean we can comment on the potential applicability of studies such as this. For example, the expected gain in bole biomass would be approximately one-third of the difference between the mean of all clones and the mean of the selected clones. In Nordegg, if the best clones of the six were selected, this could mean a gain of 9.2 kg per stem. In Blue Ridge the gain could be as much as 43.9 kg per stem. Based on mean numbers of stems per hectare and the maximum potential gains mentioned above, biomass at 85 years could be increased by 17 885 kg/ha at Nordegg and 58 124 kg/ha at Blue Ridge. These figures represent a 20% increase at Nordegg and a 16% increase at Blue Ridge on an areal basis.

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